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Global Motion Perception: No Interaction Between the First- and Second-order Motion Pathways

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The experiments reported here address the issue of whether the pathways which extract motion from first-order and second-order spatial patterns remain separate or whether they combine at some higher level in the motion system to form a single pathway. The question is addressed by investigating the interaction of first-order and second-order stimuli in the processing of a global-motion stimulus [a variant of the task introduced by Newsome & Pare (*Journal of Neuroscience*, *8*, 2201–2211, (1988)]. Two experimental procedures were used. The first consisted of determining the effect of the addition of dots of one type (e.g. first-order) undergoing purely random motion on the ability to extract the global-motion signal carried by dots of the other type (e.g. second-order). The second experimental procedure consisted of determining the effect of maintaining a coherent-motion signal in one type of dot, moving in the opposite direction to the global-motion direction, on the ability to extract the global-motion signal carried by dots of the other type. The dots were matched for their effectiveness in producing a global motion percept and the results for both procedures were the same. First-order dots impaired the ability to extract second-order global-motion, and second-order dots had no effect on first-order global-motion extraction. It is argued that the sensitivity of the second-order global-motion system to the first-order dots is due to the ability of the second-order local-motion detectors to detect these dots. The present results are thus interpreted as indicating that the first-order and second-order motion pathways remain separate up to and including the level in the motion system at which global-motion signals are extracted.

Global motion Motion Second-order motion

INTRODUCTION

In studies of motion perception, it has proven useful to categorise stimuli as being either first-order or second-order (Cavanagh & Mather, 1989). First-order stimuli are defined by differences which may be extracted by linear operators, e.g. variations in luminance or colour. Second-order stimuli are defined by variations in these first-order properties, examples of which are contrast-defined and texture-defined stimuli (Badcock & Derrington, 1985; Chubb & Sperling, 1988, 1989; Cavanagh & Mather, 1989; Pantle & Turano, 1992).

Derrington and Badcock (1985) demonstrated that motion thresholds of first-order and second-order stimuli have different dependencies on stimulus parameters. They proposed that distinct detection processes were required for the two classes of stimuli. This notion has since been supported by findings that first- and second-order stimuli cannot interact to produce a percept of apparent motion (Ledgeway & Smith, 1993; Nishida & Sato, 1993; Mather & West, 1993). Wilson, Ferrera and Yo (1992) developed a model of first- and second-order motion in which separate pathways exist for the two stimulus classes. Such a model is supported by the findings of Solomon and Sperling (1994) that observers are able to simultaneously determine the direction of motion of first-order and second-order stimuli that are matched for spatial frequency and speed.

Support for separate first-order and second-order pathways is provided by the finding that observers are able to simultaneously determine the direction of motion of first-order and second-order stimuli that are matched for spatial frequency and speed (Solomon & Sperling, 1994). Additional support comes from the neurological patient F. D. Vaina, LeMay and Grzywacz (1993) found that the performance of this patient on second-order motion tasks was severely impaired, while his performance on first-order motion tasks was normal.

The question arises as to whether these first- and second-order pathways remain separate or whether they combine to form a single motion pathway. Wilson *et al.*

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(1992) used a plaid pattern, that contains both first- and second-order stimulus characteristics, to investigate this question. They proposed that first-order stimuli are primarily processed by cortical visual area V1 while second-order stimuli also require processing by V2. This additional processing causes a delay before second-order stimuli are available to the system. Derrington, Badcock and Henning (1993) have provided psychophysical evidence for this delay. The outputs of these two regions are then combined at a higher level in the motion pathway Wilson *et al.* proposed that this occurs in cortical area MT. At this point there is only a single motion pathway in their model; one which combines inputs from both the first- and second-order motion pathways. Such a model is supported by Albright's (1992) neurophysiological finding that most cells in area MT are sensitive to both first- and second-order stimuli.

Area MT serves an important role in motion processing since it appears to be the area at which the output of the initial motion units are integrated or compared (see Movshon, 1990 for a review). An example of motion task that requires this form of comparison is the extraction of the 2-dimensional motion vector in plaid motion (Wilson *et al.*, 1992).

We investigated the notion of a common high-level first- and second-order motion pathway by using a different high level motion task to Wilson *et al.* (1992): a modified version of Newsome and Pare's (1988) global dot-motion stimulus. This stimulus is essentially a modified multi-frame random-dot pattern in which only a small number of dots, the signal dots, move in the global motion direction, while the others, the noise dots, move in random directions.

A feature of this type of stimulus is that the signal dots are randomly chosen at the start of each frame. Thus, for example, while 10 dots may be carrying the signal from one frame to the next, a different set of dots will be carrying the signal in the next frame transition. This means that for low signal levels, the probability that the same dot will carry the global motion signal over successive frames is quite low. For example, if the signal level is 10% the probability that a particular dot will carry the signal over two successive frames is 1%. Thus at low signal levels local motion cues over a series of frames are not, in isolation, effective in establishing the global-motion direction. Instead, motion information must be integrated over the entire spatio-temporal viewing aperture.

The threshold measure is the minimum number of signal dots required to determine the global-motion direction. Thus the extraction of a global-motion direction can be thought of as the attainment of a required signal-to-noise ratio—where the signal is the number of motion vectors in the global-motion direction and the noise is the number of motion vectors in all other directions. As such, global-motion extraction can be considered as a two-stage motion process. The first stage is the extraction of the local-motion vectors. For the motion extraction of the first-order spatial patterns, this involves some form of motion energy extraction (Adelson & Bergen, 1985) and is probably performed by the motion sensitive cells in V1. Motion extraction of the second-order spatial patterns involves an additional step (Chubb & Sperling, 1988) which Wilson *et al.* (1992) argue is performed by motion sensitive cells in area V2. The second stage is the integration/comparison of these local-motion signals in order to extract the global-motion direction. Such a task is well suited to the apparent function of MT (Movshon, 1990). Indeed, lesion studies (Newsome & Pare, 1988), human clinical studies (Baker, Hess & Zihl, 1991; Vaina, Lemay, Bienfang, Chol & Nakayama, 1990) electro-microstimulation studies (Salzman, Britten & Newsome 1990) and transcranial magnetic microstimulation studies (Hotson, Braun, Herzberg & Boman, 1994) have shown that the middle temporal (MT) area is important in the processing of the global dot-motion stimulus.

By using a version of this task which contains first- and second-order dots, we should be able to psychophysically test whether there is a single motion pathway, sensitive to first- and second-order stimuli, or whether there are separate first- and second-order motion pathways at the level in the motion pathway at which the global-motion signal is extracted.

Two experimental procedures were used to investigate the interaction of the first- and second-order motion pathways in global-motion analysis. The first procedure used a motion-noise approach. This approach consists of determining whether adding dots of one type interferes with the processing of the global-motion signal carried by dots of the other type (Experiments 1 and 2). The second procedure extends this approach by the addition of a coherent signal in the "noise" dots, to determine whether global-motion signals carried by one dot type can interfere with the global-motion signal carried by dots of the other type (Experiment 3). These two procedures have been previously used by us to investigate the interaction of the On and Off pathways in global-motion extraction (Edwards & Badcock, 1994).

EXPERIMENT 1: EFFECT OF SECOND-ORDER STIMULI ON FIRST-ORDER SIGNAL EXTRACTION

The procedure used in this experiment to investigate the effect of a second-order stimuli on first-order motion extraction is based on the finding that as dot density is increased (thus increasing the number of local-motion vectors) the number of signal dots that an observer needs in order to be able to determine the global motion direction also increases (Edwards & Badcock, 1994a). Three experimental conditions were used in which the number of first-order and second-order dots were varied (stimulus details are given below). They were: (i) 50 first-order dots; (ii) 100 first-order dots; and (iii) a combined stimulus using 50 first-order and 50 second-order dots. In condition (iii), only the first-order dots carried the global-motion signal; the second order dots were always noise dots.

If there are separate first-order and second-order global-motion systems, then adding the pure-noise second-order dots should have no effect on first-order global-motion extraction. That is, the threshold for the condition containing 50 first-order and 50 pure-noise second-order dots, [Condition (iii)] should be the same as the condition containing only 50 first-order dots, [Condition (i)]. However, if the first-order and second-order motion pathways are pooled prior to global-motion extraction, and if this single globalmotion system is equally sensitive to the first- and second-order dots, then the threshold for Condition (iii) should be the same as for the condition containing 100 first-order dots, [Condition (ii)]. Clearly an important step in this argument is the matching of the contrasts of the first- and second-order dots. This issue is addressed below.

Method

Observers. Four observers were used, with three of these observers being naive with respect to the aims of this research, while the other was one of the authors. All had normal acuity with no history of visual disorders.

Stimuli. The stimuli consisted of an 8 frame global dot-motion sequence. The duration of each frame was 50 msec, with no inter-frame interval being used, giving a total stimulus duration of 400 msec. The spatial step size was 0.3°, resulting in a stimulus speed of 6°/sec. This speed is in the optimum reported speed range of MT cells (Lagae, Raiguel & Orban, 1993; Maunsell & Van Essen, 1983). Each dot was circular, subtended 0.2 deg of visual angle, and was composed of 13 pixels. The viewing aperture was a 12° diameter circle, and the number of dots was either 50 or 100, resulting in dot densities of 0.44 and 0.88 dots/deg^2. This combination of dot density and spatial step size resulted in a low probability of false motion signals occurring (Williams & Sekuler, 1984). The background consisted of a static random-pixel field, at 10% luminance contrast, with a mean luminance of 17.6 cd/m^2. The luminance beyond the viewing aperture was less than 1 cd/m^2.

As stated above, three conditions were used: (i) 50 first-order dots; (ii) 100 first-order dots; and (iii) a combined stimulus using 50 first-order and 50 second-order dots in which the second-order dots were always noise dots.

In setting the luminance values of the first- and second-order dots, it was important to ensure that they were of equal strength. A common way to equate stimuli is to make them equal multiples of their respective detection thresholds (Cropper & Derrington, 1994; Smith, Hess & Baker, 1994). Such an approach, however, makes a number of assumptions that, in this situation at least, are not necessarily valid. These assumptions are that the contrast response functions for the system/s which process both stimuli are the same, and that the system of interest—in this case the global-motion system—is the system involved in the detection of the presence of the stimulus; and hence that detection thresholds are the relevant measure of the effectiveness of the stimuli in driving the global-motion system.

Since these assumptions are not necessarily valid for this task, and since the threshold measure used in the present experiments was the required number of signal dots, we matched the luminance contrasts of the first- and second-order stimuli on the basis of global-motion thresholds. That this appears to be a valid way to match the stimuli is discussed later, in light of the data.

We have previously investigated how performance for both first- and second-order global-dot motion depends on luminance contrast (Edwards & Badcock, 1995). For first-order stimuli and second-order stimuli on a static background, performance initially improved with increasing contrast until a saturation point was reached. In the present experiments, the luminance contrasts of the first- and second-order dots were set so that they were in their respective saturation regions. While this ensures that both classes of stimuli were in their optimum range, it does not necessarily ensure that they result in comparable performance. Consequently, first- and second-order thresholds were checked at the completion of Experiment 2. As will be discussed in Experiment 2, for three of the observers, thresholds for first- and second-order motion were the same.

The second-order dots were composed of light and dark pixels at 90% contrast (33.4 and 1.8 cd/m^2). Each pixel had an equal probability of being either light or dark, so that averaged over a number of motion frames, the mean luminance of each dot was the same as that of the background. The luminance of the pixels were randomly assigned at the start of each motion frame. This ensured that there was no systematic luminance (first-order) motion cue between successive motion frames due to either small differences in the mean luminance of the dot and the background, or in the luminance pattern of the dot. From previous studies (Edwards & Badcock, 1994) we know that the motion system cannot track a stimulus which changes luminance polarity. The first-order dots were luminance defined, with the luminance level being set at the value of the light pixels of the second-order dots (33.4 cd/m^2)—resulting in a contrast of 31%, relative to the mean luminance level.

Apparatus. The stimuli were displayed on a Barco CDCT6551 colour monitor, which was driven by the framestore section of a Cambridge Research Systems VSG 2/1 (thus providing 8 bit colour resolution) in a host 80386 computer. Observer responses were recorded using a button box. The display had a refresh rate of 120 Hz. Luminance calibration was performed using a Tektronix J16 photometer with a 1° luminance probe, and chromatic calibration with a Minolta Chromameter.

Procedure. A single-interval two alternative-forced-choice procedure was used. The direction of motion of the stimulus for a given trial was randomised to be either "up" or "down". Thresholds were established using a modified staircase procedure that converged on the 79% correct performance level (Badcock & Smith, 1989). Eight reversals were collected, with the threshold being taken as the mean of the last 6 reversal points. The staircase started at a signal strength of 50 dots (i.e. 50 dots moving in the same direction). The initial step size in signal strength was 8 dots, but this was decreased after each of the first three reversals, so that the step size for the last 6 reversals was 1 dot. Each threshold reported represents the mean of ten staircases.

Observers sat in a dark room, 0.71 m from the screen, with their head supported by a chin rest. Viewing was binocular, and no feedback concerning the accuracy of response was given. Only one staircase was run at a time, but staircases testing the three conditions used in the present experiment, as well as the three conditions used in Experiment 2, were randomly inter-leaved.

Results and discussion

The number of signal dots required to correctly perceive the global motion direction 79% of the time is plotted for the three conditions in Fig. 1. Error bars indicate one standard error of the mean. The pattern of results is the same for all four observers. Thresholds are the same for both the 50 first-order dots (50F) and the 50 first-order plus 50 second-order dots (50F/50S) conditions, while those for the 100 first-order dots (100F) condition are higher.

The observers task in all three conditions was to detect the global-motion signal carried solely by the first-order dots. Results show that adding the second-order noise dots had no effect on the extraction of the first-order global-motion signal, in that the thresholds for the 50 first-order, 50 second-order dots (50F/50S) condition was the same as the 50 first-order dots (50F) condition—and lower than the 100 first-order condition. This finding supports the notion that there is a distinct first-order motion pathway at the level in the motion system where global-motion signals are extracted.

EXPERIMENT 2: EFFECT OF FIRST-ORDER STIMULI ON SECOND-ORDER SIGNAL EXTRACTION

This experiment was the converse of Experiment 1 in that we investigated the effect of adding first-order stimuli on the extraction of a second-order global-motion signal.

Stimuli. Three stimulus conditions were used: (i) 50 second-order dots; (ii) 100 second-order dots; and (iii) 50 second-order and 50 first-order dots. In the Condition (iii), only the second-order dots carried the global motion signal.

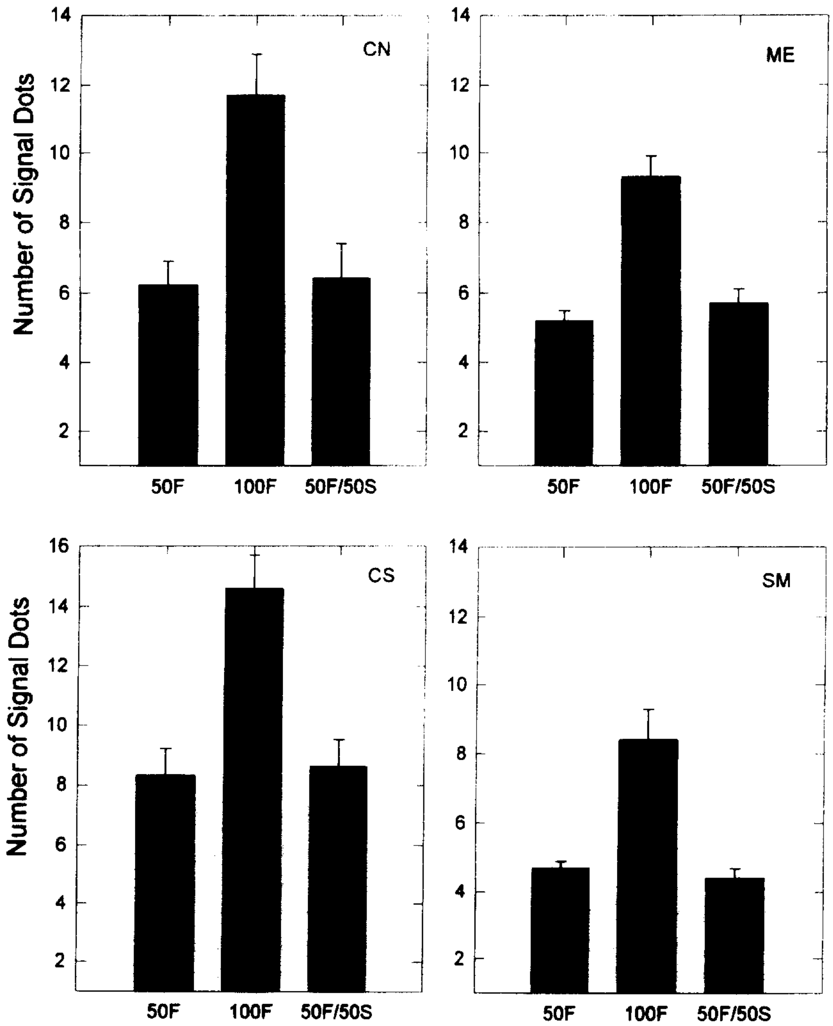

FIGURE 1. Motion thresholds for the three conditions used in Experiment 1. Condition (i) contained 50 first-order dots (50F); condition (ii) 100 first-order dots (100F); and condition (iii) 50 first-order dots and 50 second-order dots, with the signal dots being chosen only from the first-order dots (50F/50S). The pattern of results is the same for all observers. Thresholds for the 50F and 50F/50S conditions are the same and lower than the 100F condition.

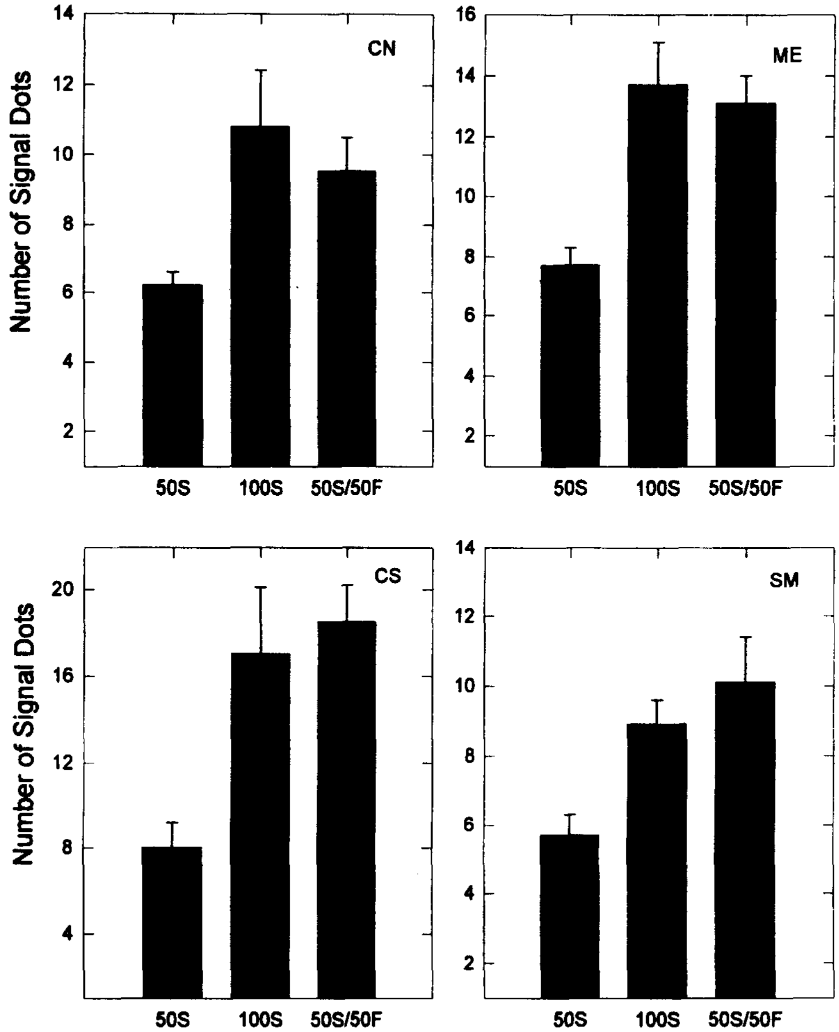

FIGURE 2. Motion thresholds for the three conditions used in Experiment 2. Condition (i) contained 50 second-order dots (50S); condition (ii) 100 second-order dots (100S); and condition (iii) 50 second-order dots and 50 first-order dots, with the signal dots being chosen only from the second-order dots (50S/50F). The pattern of results is the same for all observers. Thresholds for the 100S and 50S/50F conditions are the same and higher than the 50S condition.

Results and discussion

Thresholds for the three conditions are shown in Fig. 2. The pattern of results is the same for all four observers. Thresholds for the 100 second-order dots (100S) and the 50 second-order plus 50 first-order dots (50S/50F) conditions are the same and higher than thresholds for the 50 second-order dots (50S) condition.

The results indicate that adding the first-order noise dots affects the extraction of the second-order global-motion signal, in that the thresholds for the 50 second-order plus 50 first-order dots (50S/50F) condition was the same as the 100 second-order dots (100S) condition. Thus equivalent threshold elevations are produced by adding either 50 second-order or 50 first-order noise dots to the display.

This result, when taken with the finding of Experiment 1, indicates that there are distinct first- and second-order motion pathways at the level in the motion system at which the global-motion direction is extracted. The first-order global-motion system is sensitive only to first-order stimuli, being insensitive to second-order motion noise, while the second-order global-motion system is sensitive to both second-order and first-order stimuli used in the present experiments. This sensitivity of the second-order motion pathway to the "first-order" stimuli could be due to a number of reasons, namely: to the second-order motion detectors being sensitive to both the first- and second-order stimuli; the first-order motion pathway providing input to the second-order pathway at or prior to the level at which the global-motion direction is extracted; or a combination of the two. These possibilities are addressed more fully later.

Equating the strength of the first- and second-order dots. The luminance values used in the first two experiments were set so that the first- and second-order stimuli were in their respective saturation regions. As stated above, we aimed to match the luminance contrasts of the first- and second-order stimuli on the basis of their performance thresholds on the global-motion task. Thresholds for the conditions which contained first- and second-order dots in isolation (conditions (i) and (ii) in Experiments 1 and 2) are replotted in Fig. 3. As can be seen, for three of the subjects (CN, CS and SM) the thresholds for the respective first- and second-order conditions were the same. For these observers, if there was a single global-motion system, the first- and second-order stimuli used in the present studies would drive it with equal strength. Thus we are confident that the failure of the second-order dots to impair the extraction of the first-order global-motion signal cannot be explained in terms of a single global-motion system which is driven more weakly by the second-order dots than the first-order dots.

The fourth observer (ME) demonstrated better performance on the first-order than for the second-order stimuli. While this difference is not large, and the pattern of results is identical to that for the other three observers, this observer was retested on the conditions in the first two experiments with first-order dots defined by a lower luminance contrast. The luminance of the first-order dots was reduced to 22.5 cd/m^2, while the background and second-order luminance contrasts were kept the same (at 10%—pixel luminances of 19.4 and 15.8 cd/m^2—and 90%—33.4 and 1.8 cd/m^2, respectively). This resulted in luminance contrast (relative to the mean luminance level of 17.4 cd/m^2) of the first-order dots being 13%. At this contrast level, the thresholds for first- and second-order motion extraction were the same (Fig. 4). The results for this experiment are shown in Fig. 4. As can be seen, the pattern of results is identical to that obtained for the high-contrast first-order dots in Experiments 1 and 2—adding second-order dots does not impair the extraction of first-order motion, while first-order dots impairs the extraction of second-order motion—thus further supporting the notion that there are separate first- and second-order global-motion systems.

EXPERIMENT 3: OPPOSING-VECTOR CONDITIONS

The aim of this experiment was to verify the findings of Experiments 1 and 2 by the use of a different experimental procedure. The first two experiments investigated the interaction of first- and second-order stimuli in global-motion perception by using a noise approach—that is determining whether the addition of noise dots (and hence noise motion vectors) of one type (first- or second-order) affected the extraction of the global-

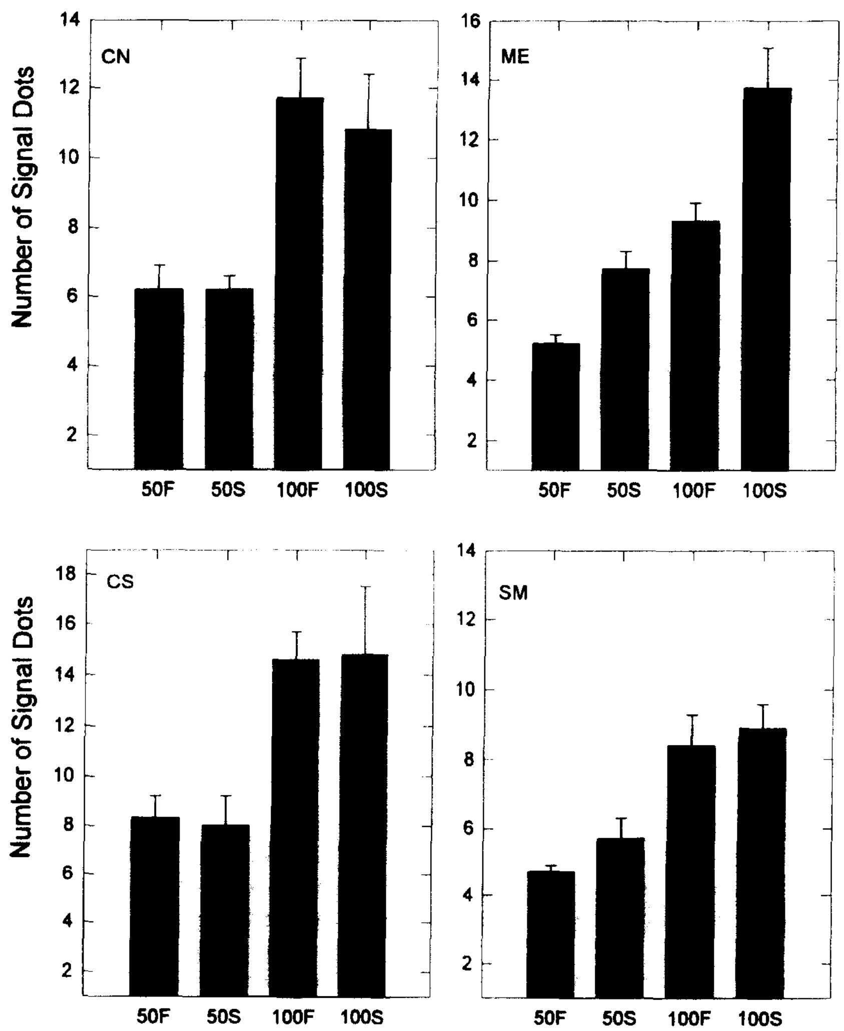

FIGURE 3. Motion thresholds for the conditions which contained first- and second-order dots in isolation (conditions (i) and (ii) in Experiments 1 and 2). For three of the subjects (CN, CS & SM) thresholds for the corresponding first- and second-order conditions (50F and 50S, 100F and 100S) are the same. The fourth observer (ME) demonstrated better performance for the first-order conditions than for the second-order conditions.

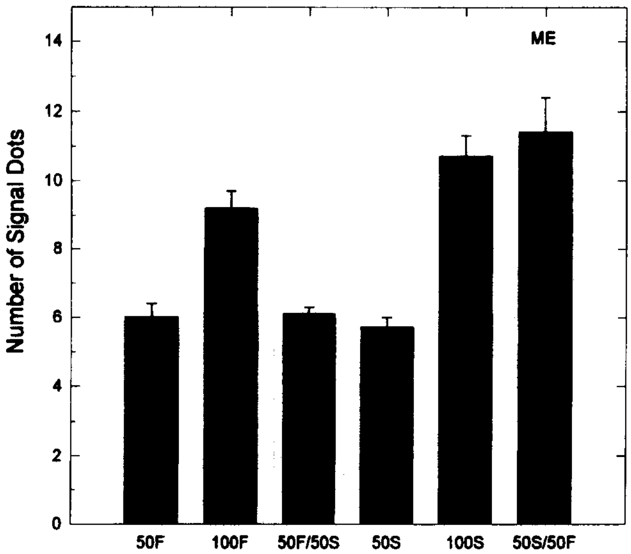

FIGURE 4. Motion thresholds for observer ME retested on the conditions used in Experiments 1 and 2 using lower contrast first-order dots. The pattern of results is identical to that obtained for the high-contrast first-order dots in Experiments 1 (Fig. 1) and 2 (Fig. 2). Additionally, the thresholds for the corresponding first- and second-order conditions are now the same.

motion carried by signal dots of the other type (second- or first-order). This experiment extended that approach by the inclusion of a motion signal to the added dots.

The addition of a motion signal, equal in strength to, and moving in the opposite direction to a global-motion signal (an opposing-vector signal) results in the perception of transparent motion of the two motion signals. If these two signals (global-motion and opposing-vector) are carried by dot types which are processed by the same global-motion system, then the observer will not be able to identify which signal (global motion or opposing vector) is going in which direction. Under such conditions, it is not possible for the observer to determine the global-motion direction (Edwards & Badcock, 1994). The strength of the global-motion signal has to be increased until the observer is able to identify the (stronger) global-motion signal. That is the addition of an opposing-vector signal carried by a dot type which is processed by the same global-motion system which processes the global-motion dots results in the elevation of global-motion thresholds.

If, however, the two signals are carried by dot types which are processed by different global-motion systems, then an observer should be able to identify the direction of motion of the different dot types and hence not need differences in signal strength to differentiate them. That is, the addition of an opposing-vector signal carried by a dot type which is processed by a different global-motion system to the one which processes the global-motion dots should not result in an elevation in global-motion thresholds.

This procedure therefore provides an additional approach to investigate the degree of independence in the processing of first- and second-order signals in global-motion perception. One which is based upon the interaction of global-motion signals.

Observers. Two of the observers used in the previous experiments (CN and ME) served as observers in this experiment, and CN was naive with respect to the experimental aims.

Stimuli. Two stimulus conditions were used. The first condition comprised 50 first-order and 50 second-order dots, as in condition three of Experiment 1, except that a fixed second-order signal was presented in the opposite direction to the global-motion direction. The strength of this opposing-vector second-order signal was set at the particular observer's threshold for the 50 first-order plus 50 second-order dots condition [Experiment 1, Condition (iii)]. This was equal to 6 dots for both observers. The required number of first-order dots moving in the global-motion direction was established using a staircase procedure as in the previous experiments. The second condition was the converse of the first, comprising 50 second-order dots and 50 first-order dots, with the global-motion signal being carried by the second-order dots and a first-order opposing-vector signal. As with the first condition, the number of opposing-vector first-order dots was set at 6.

To be consistent with the results of Experiments 1 and 2, the addition of the second-order opposing-vector signal should have no effect on first-order global-motion extraction, while the first-order opposing-vector condition should elevate second-order global-motion thresholds.

In accordance with the previous arguments concerning the matching of the first- and second-order stimuli, the luminance contrast for the first-order dots for observer CN was set at 31%, and for ME, at 13%. The contrasts of the background and second-order dots were as in the previous experiments, 10 and 90% respectively.

Results and discussion

The results for the two current conditions, as well as condition three from the first two experiments, are shown in Fig. 5. The pattern of results is the same for both observers. For the two conditions where the global-motion signal was carried by the first-order dots (50F/50S conditions) the threshold (number of first-order signal dots) for the condition with the 6 second-order opposing-vector dots (S-Opp) is the same as the threshold for the condition in which there is no second-order opposing-vector dots* (Non-Opp). For the two conditions where the global-motion signal is carried by the second-order dots (50S/50F conditions) the threshold (number of second-order signal dots) for the condition with 6 first-order opposing-vector dots (F-Opp) is higher than the threshold for the condition in which there is no first-order opposing-vector dots† (Non-Opp). Additionally, the threshold for condition

*Note, this condition is the same as the 50F/50S condition in Experiment 1.

†Note, this condition is the same as the 50S/50F condition in Experiment 2.

F-Opp is higher than the threshold for condition Non-Opp by a value of approx. 6—the number of first-order opposing-vector dots.

The results of the present experiment (Fig. 5) shows that adding a second-order opposing-vector signal had no effect on the extraction of a first-order global-motion signal, while an opposing first-order signal had an effect on the extraction of the second-order signal. Specifically elevating the threshold by an amount approximately equal to the number of second-order opposing-vector dots (6). These results are consistent with the predictions, made above, which were based on the findings of the first two experiments. These findings therefore support the notion that there are (at least) two distinct global-motion systems, and that the first-order system is sensitive only to first-order stimuli, while the "second-order" system is sensitive to both first- and second-order stimuli.

An additional finding in the present experiment is that the increase in the threshold for second-order motion extraction in the presence of opposing-vector first-order dots was approximately equal to the number of those first-order dots. This supports our earlier claim that, as far as global-motion extraction is concerned, the second-order global-motion system has equal sensitivity to our first- and second-order dots.

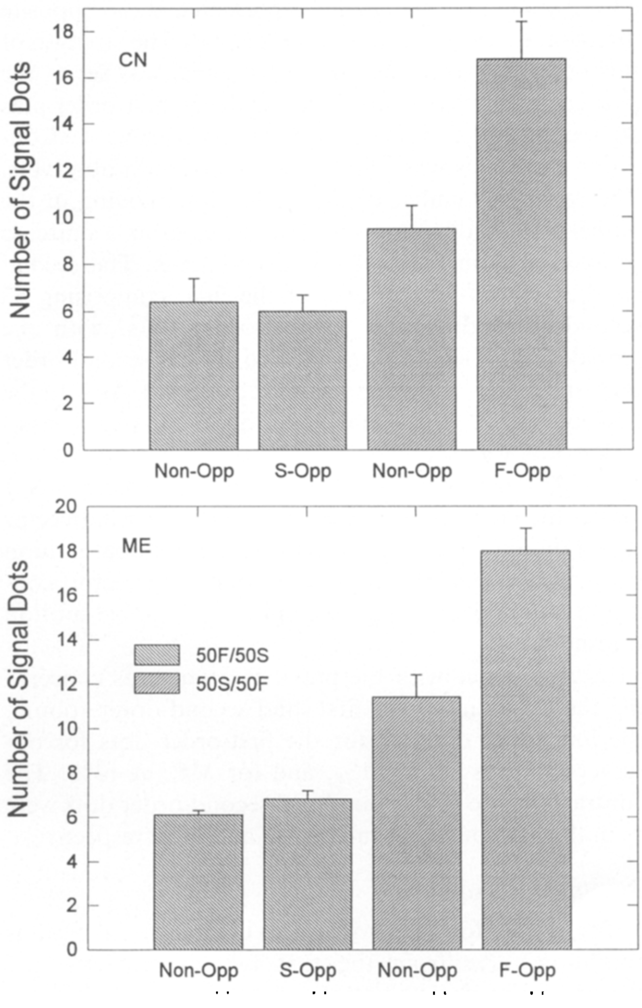

FIGURE 5. Motion thresholds for the conditions used in Experiment 3. Two conditions were used. The first comprised 50 first-order and 50 second-order dots, with 6 second-order dots moving in the opposite direction to the first-order global-motion dots (S-Opp). The second condition comprised 50 second-order and 50 first-order dots, with 6 first-order dots moving in the opposite direction to the second-order global-motion dots (F-Opp). For purposes of comparison, the thresholds for condition three from the first two experiments are also shown—50 second-order and 50 first-order dots with the signal dots selected from the first-order dots (Non-Opp, previously labelled 50F/50S, Fig. 1) and 50 second-order and 50 first-order dots, with the signal dots selected from the second-order dots (Non-Opp, previously labelled 50S/50F). The pattern of results is the same for both observers. Thresholds for the S-Opp and 50F/50S Non-Opp conditions are the same, while the threshold for condition F-Opp is greater than that for 50S/50F Non-Opp—by an amount about equal to the number of opposing-vector first-order dots (6).

GENERAL DISCUSSION

The conclusions of the present study are that there is a separate first-order global-motion system, sensitive only to first-order stimuli, and a "second-order" global-motion system sensitive to both first- and second-order stimuli used in the present study. These conclusions are based on the findings that: (1) adding pure-noise second-order dots had no effect on the extraction of a first-order global-motion signal; (2) adding pure-noise first-order dots had an adverse effect on the extraction of a second-order signal; (3) a second-order opposing-vector has no effect on first-order global-motion extraction; and (4) a first-order opposing-vector impairs second-order global-motion extraction.

Interaction of first- and second-order pathways

The results of the present experiments support a number of conclusions about the global-motion system. The first is that, as Wilson *et al.* (1992) and Mather and West (1993) have argued, there exist distinct first-order and second-order motion pathways. Furthermore, these pathways appear to remain distinct up to and including the area at which global motion is extracted—though see discussion below with respect to the second-order pathway. If, as noted in the Introduction, the area where the global-motion direction is extracted is MT, the present finding appears to be contrary to Wilson *et al.*'s claim that the first- and second-order motion pathways combine to form a single pathway at the MT level. However, area MT has been found to be a functionally inhomogeneous area (Born & Tootell, 1992; Krubitzer & Kaas, 1990) so it is possible that integration of the first- and second-order pathways occurs in one of these subregions.

It is worth noting that the present findings are compatible with the findings of Albright (1993)—that most of the cells he recorded from in area MT were sensitive to both first- and second-order stimuli, with the remainder sensitive only to first-order stimuli since it is possible that he was recording mainly from the cells in the second-order pathway.

Results due to differences in processing speed?

One anonymous reviewer raised the possibility that the pattern of results obtained in the present study is due to the different processing speeds of the first- and second-order motion signals. In the Introduction it was noted that the additional processing required for second-order motion extraction results in a delay, relative to the first-order information, before the second-order information is available to the motion system. Thus, at least in theory, the present results could be accounted for by proposing a single global-motion system, combining both first- and second-order inputs, in which the second-order signals are delayed relative to the first-order. This would allow the first-order information to be extracted prior to the arrival of the second-order information, so that adding second-order dots would have no effect on first-order global-motion extraction, while the addition of first-order dots would affect second-order global-motion extraction.

To be valid, this explanation requires the extraction of the first-order global-motion information prior to the arrival of the second-order information. Evidence will now be presented to show that the achievement of such a requirement is not possible. Wilson *et al.* (1992) incorporate a 60 msec time delay in the processing of second-order motion in their model. The inclusion of this delay results in the output of their model closely approximating the observed changes in the perceived direction of high luminance-contrast Type II plaids as a function of time (Yo & Wilson, 1992).

Watamaniuk and Sekuler (1992) have shown that thresholds for the Williams and Sekuler (1984) version of the first-order global dot-motion task improve as the number of frames in the motion sequence is increased. This improvement continues up to 9.3. The duration of each motion frame in their study was the same as that used in the present, 50 msec. This gives a temporal integration time for first-order global-motion extraction of 465 msec. Figure 6 shows how thresholds vary as a function of the number of motion frames in the version of the global dot-motion stimulus used in the present study. The stimulus consisted of 100 first-order dots on a uniform luminance background at 17.6 cd/m^2. The contrast of the dots was 17% and all other temporal and spatial parameters were the same as those used in the previous experiments. The range of motion frames tested was 2–8. Observer ME is still showing an improvement in thresholds at 8 frames duration, while SM seems to have reached stable performance by about 7 frames of motion. The important aspect of these results for the present argument is that for 3 frames of motion, thresholds for both observers are about twice their thresholds for 8 frames of motion. Given that 3 frames of motion corresponds to a stimulus duration of 150 msec (compared to proposed processing delay for the second-order pathway of about 60 msec), and that the difference between the 50 and 100 dot conditions in Experiments 1 and 2 were in the order of a factor of 2, it would not be possible to achieve the first-order motion thresholds in the combined first- and second-order conditions prior to the delayed arrival of the second-order motion signal in a single global-motion model.

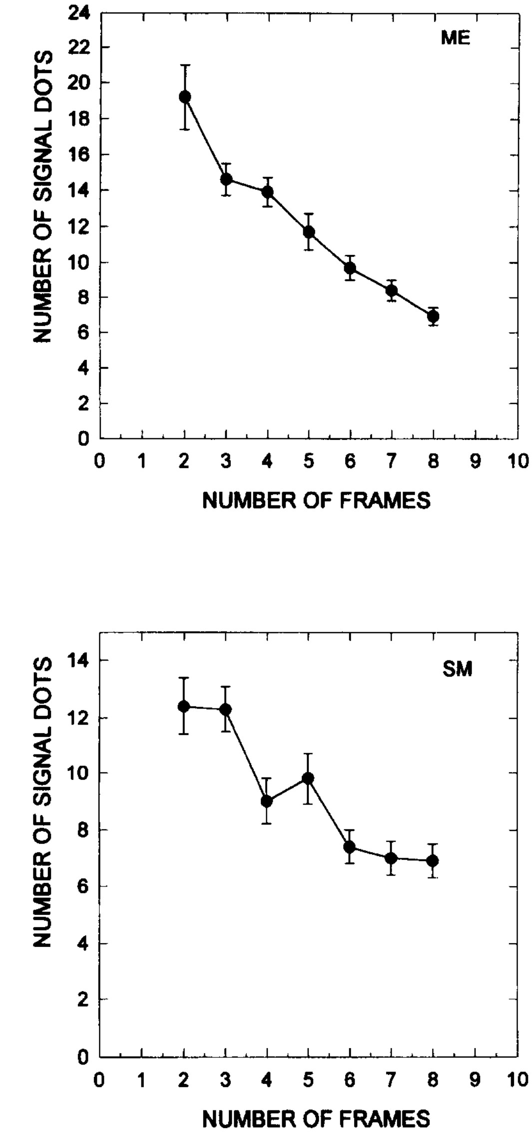

FIGURE 6. Motion thresholds for first-order global-motion extraction as a function of the number of frames in the motion sequence. Observer ME is still showing improvement in performance at 8 frames of motion, while SM's performance is relatively stable by about 7 frames. For both observers, thresholds at 3 frames of motion are about twice their threshold for 8 frames of motion.

Stimulus sensitivities of the first- and second-order pathways

As expected from the design of the stimuli, the first-order pathway is sensitive only to the first-order stimuli in the present study. This is consistent with the standard models of first-order motion extraction (Reichardt, 1961; Adelson & Bergen, 1985).

The "second-order" pathway is sensitive to both the first-order and second-order stimuli used in the present study. There are (at least) three possible models which would account for this finding. In considering these models it is important to keep in mind the two stage nature of the global-motion task, as discussed in the Introduction. The first stage is the extraction of local-motion signals and the second stage is the integration/comparison of these local-motion signals in order to extract the global-motion signal. This second-stage process can be thought of as the attainment of a required signal-to-noise ratio—where the signal is the number of motion signals in the global-motion direction and the noise is the number of motion signals in other directions.

The three possible models accounting for the sensitivity of the second-order global-motion system to the first-order stimuli used in the present study are:

(1) The second-order local-motion detectors are sensitive to both the first- and second-order stimuli employed in the present study, and the second-order global-motion system receives input only from these second-order local-motion detectors.

(2) The second-order local-motion detectors are sensitive only to second-order stimuli, and the second-order global-motion system pools signals from first- and second-order local-motion detectors.

(3) A combination of models 1 and 2, in which the second-order local-motion detectors are sensitive to both first- and second-order stimuli, and the second-order global-motion system pools inputs from first- and second-order local-motion detectors.

While the results of the experiments conducted in the present study allow us to establish the existence of separate first- and second-order global-motion systems, they do not allow us to determine which of the above models accounting for the second-order global-motion system's sensitivity to first-order stimuli is correct. However we argue that Model 1 is the most plausible.

Model 2 seems unlikely since the second-order motion detectors that have been proposed would also be sensitive to the first-order stimuli used in the present study. Examples of such models are those proposed by Chubb and Sperling (1988), Wilson *et al.* (1992) and Zhou and Baker (1993). The Chubb and Sperling model consists of halfwave or fullwave rectification prior to motion-energy extraction, while the models proposed by Wilson *et al.* and Zhou and Baker consist of 4-stages, bandpass spatial filtering centred on a high spatial frequency, squaring or rectification, further bandpass filtering centred on a low spatial frequency (at an orientation that is orthogonal to the initial filtering in the Wilson *et al.* model), and then motion-energy extraction.

Any luminance stimulus would drive the Chubb and Sperling model (except a stimulus in the general class of rectangular-wave gratings in the fullwave rectification version of the model) while only stimuli that are spatially localised and have a broad spatial frequency bandwidth would get past both filtering stages in the 4-stage models. The spatial-frequency bandwidth of the first-order dots used in the present study should be broad enough to enable them to drive the 4-stage models. To test this hypothesis we determined the result of passing a number of stimuli, including the first-order dots, through a version of the 4-stage motion model. The version used was a variation of the Wilson *et al.* (1992) model. It consisted of an initial gabor filter, halfwave rectifier and a second gabor filter, with the second gabor filter having a gaussian with twice the standard deviation and a sinewave with half the spatial frequency and at an orientation of 90° to those used in the first gabor filter. This filter was convolved with four stimuli: a first-order dot; a second-order dot (both on contrast defined background as used in the present study); a uniform contrast-defined background; and a full-field sinewave grating (see the Appendix for further details).

The output of this convolution with the four stimuli is shown in Figs 7–10. In all of the Figures, (a) represents the stimulus, (b) the activity map following the convolution, and (c) the histogram of the activity map. The grey scale used in (b) indicates the response magnitude; white maximum positive response, black maximum negative response and grey no response. While the filter gives the greatest response to the second-order dot (Fig. 8) it also gives a response to the first-order dot (Fig. 7). The response to these two dot types can be best determined by comparing their response histograms to that for the uniform background (Fig. 9). The response histograms give the relative number of pixels at each response intensity level. The uniform background results in a response profile given by the unimodal distribution in Fig. 9(c). The response to the first-order and second-order dots in Figs 7(c) and 8(c), respectively are thus indicated by the activity levels above and below the unimodal distribution.

As can be seen from Fig. 10, a full-field sinewave does not result in any response. The frequency of the sinewave was matched to the sinewave in the first gabor, so while it was able to be passed by the high-centre-frequency bandpass first filter, following halfwave-rectification, its energy was predominantly at the high spatial frequencies and it was therefore unable to be passed by the second filter, which had a low centre-frequency bandpass filter and an orientation that was 90° to the first filter. If the second-order motion system employed a processing sequence similar to that described here, then the difference in the response to the first-order dots and first-order full-field sinewaves may account for the seemingly contradictory results obtained by Ledgeway and Smith (1993). Unlike the present finding that the second-order pathway is sensitive to our first-order dots, Ledgeway and Smith (1993), using a first-order sinewave, and found no interaction between first- and second-order stimuli.

Models 1 and 3 differ on the issue of whether the second-order global-motion system receives input from first-order-motion units. A strong argument can be made for the notion that the second-order system does not receive first-order input. This argument is based on the notion that the extraction of a global-motion signal requires the attainment of a critical signal-to-noise ratio, and feeding the first-order motion signals into the second-order global-motion system would only serve to increase the noise associated with second-order motion extraction. This increase in noise is due to the fact that many second-order motion stimuli result in

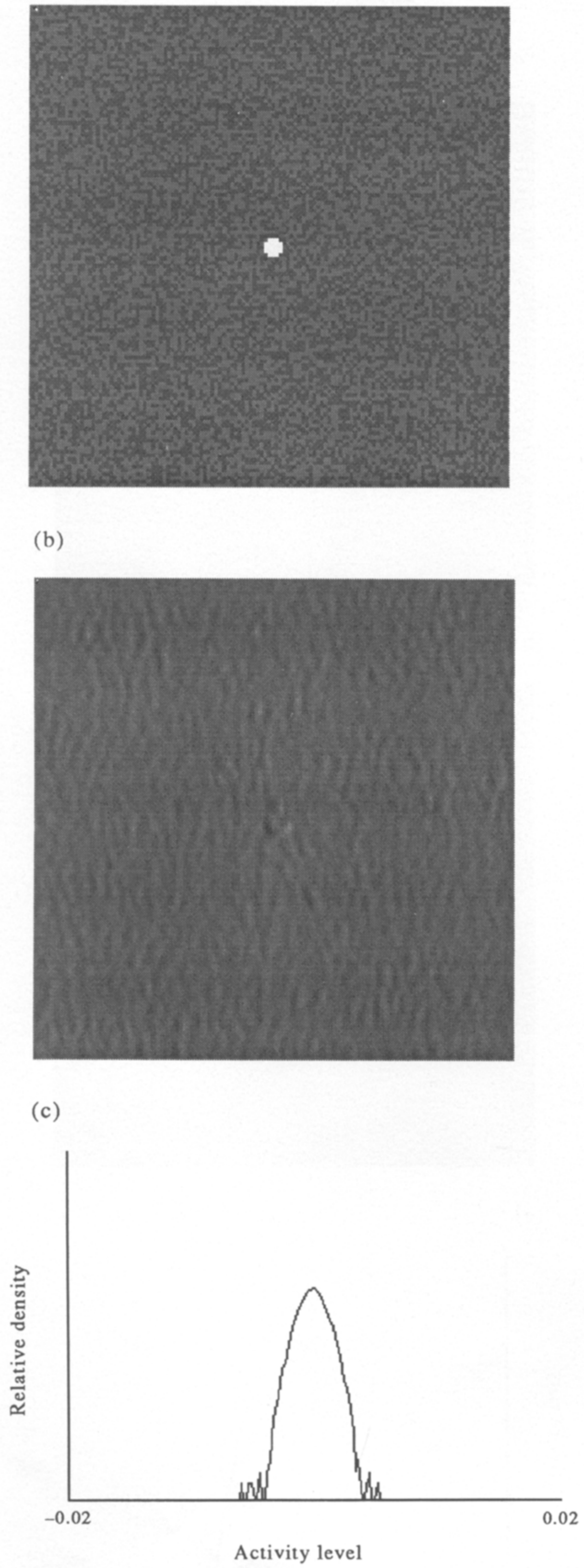

FIGURE 7. A luminance-defined first-order stimulus and the result of processing it with the first three stages (filtering, halfwave rectification and refiltering) of the four-stage motion model described in the Appendix. (a) Depiction of the first-order stimulus. (b) The activity map resulting from the processing. The grey scale indicates the response magnitude; white represents the maximum positive response, black the maximum negative response and grey no response. (c) Histogram of the activity map. The response to the dot is indicated by the activity levels lying either side of the central unimodal distribution.

a pure noise signal in the first-order motion domain. The number of first-order random-motion vectors can be extremely high, which would make the attainment of the required signal-to-noise ratio for second-order motion extraction particularly difficult, if first-order motion signals were fed into the second-order system. An example of a second-order stimulus which results in an extremely high number of first-order noise vectors is the second-order motion stimulus as used in the present experiment when a dynamic background is present. That is, like the luminance of the pixels making up the dots, the luminance of the pixels making up the background is randomly assigned at the start of each motion frame. The thresholds for such a stimulus are comparable to those for the second-order stimuli with a static background (Edwards & Badcock, 1995)—though to achieve these low thresholds for the dynamic background condition requires a high contrast difference between the dots and the background. Such a result would be unlikely if the first-order local-motion units provided input to the second-order global-motion system.

Equation of the strength of the first-order and second-order dots

We interpret the present results (that second-order dots do not effect first-order global-motion extraction, while first-order dots effect second-order global-motion extraction) as indicating the existence of separate first-order and second-order global-motion systems and that the second-order system is sensitive to the (broad frequency bandwidth) first-order stimuli used in the present study. However, another possible interpretation of the results is that there is a single global-motion system, sensitive to both first- and second-order stimuli, and that we failed to correctly match the relative strengths of the first-order and second-order dots. Specifically that the (single) global-motion system is more sensitive to the first-order dots than the second-order dots used in the study. While this may account for the finding that the second-order dots failed to impair first-order global-motion extraction while the first-order dots did impair second-order global-motion extraction, the suggestion is not consistent with other aspects of the present findings. Before going into these aspects, it is worth restating the approach used in the present study to equate the relative strengths of the first-order and second-order stimuli.

As noted in the Introduction to Experiment 1, the approach used in the present study to equate the relative strengths of the first- and second-order dots was to ensure that the dot-contrasts employed resulted in the same global-motion thresholds for the extraction of both first-order and second-order signals. That is the thresholds for the 50 first-order dots condition was the same as the 50 second-order dots condition (the same contrasts also yield equivalent thresholds for the 100 first-order and 100 second-order dot conditions). We argue that this is the most effective way to ensure that the two dot types are matched since if there is only one global-motion system, sensitive to both first- and

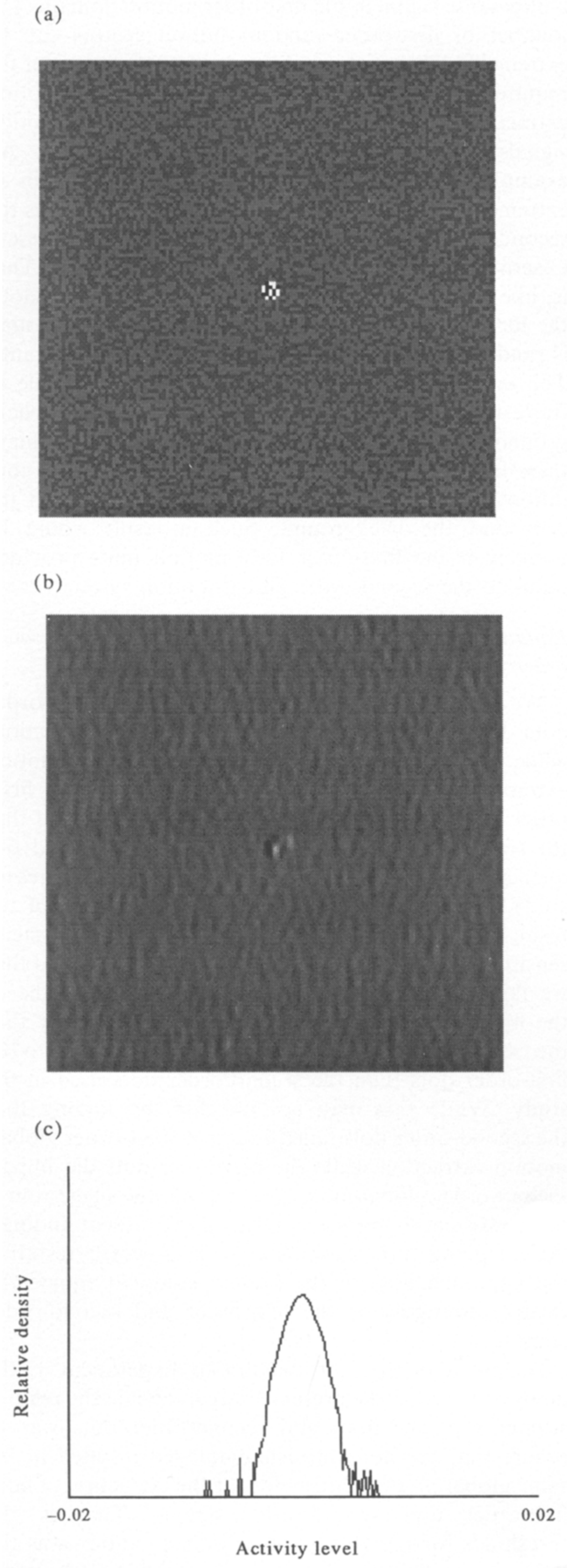

FIGURE 8. A contrast-defined second-order stimulus and the result of processing it with the first three stages of the motion model described in the Appendix. (a) Depiction of the second-order stimulus. (b) The activity map resulting from the processing. (c) Histogram of the activity map. The response to the dot is indicated by the activity levels lying either side of the central unimodal distribution.

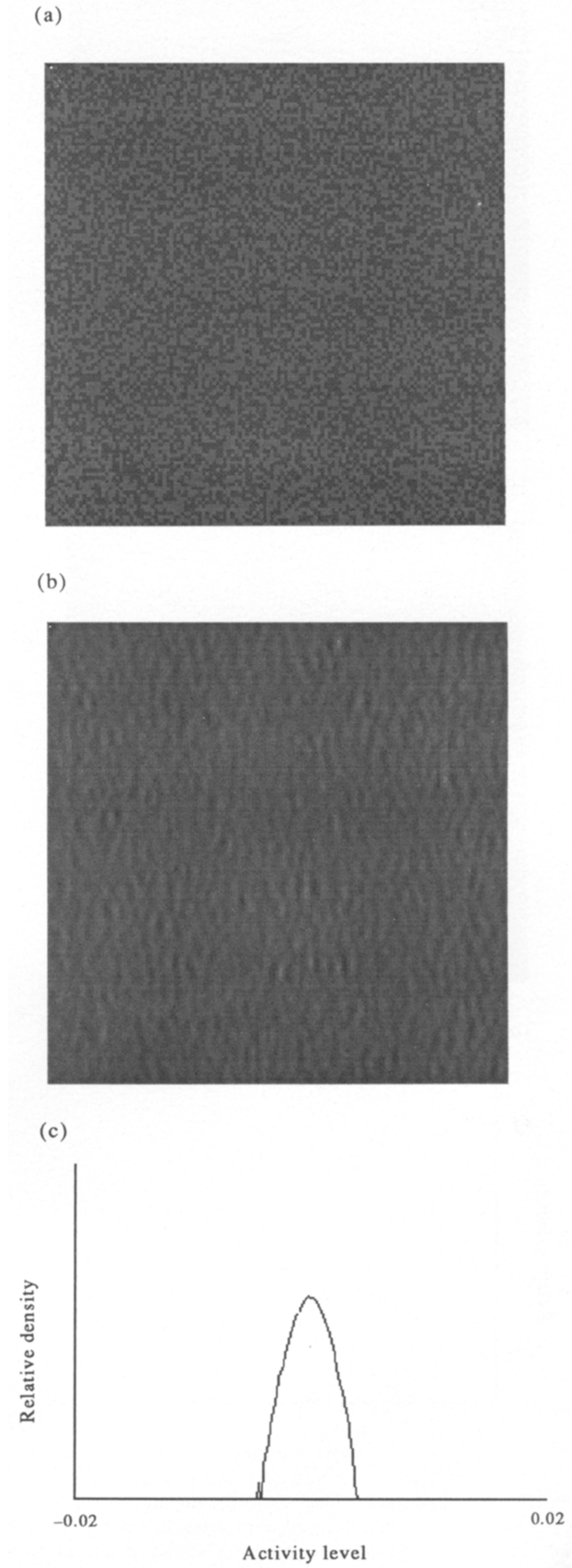

FIGURE 9. Uniform contrast-defined second-order background and the results of processing it with the first three stages of the motion model described in the Appendix. (a) Depiction of the second-order stimulus. (b) The activity map resulting from the processing. (c) Histogram of the activity map.

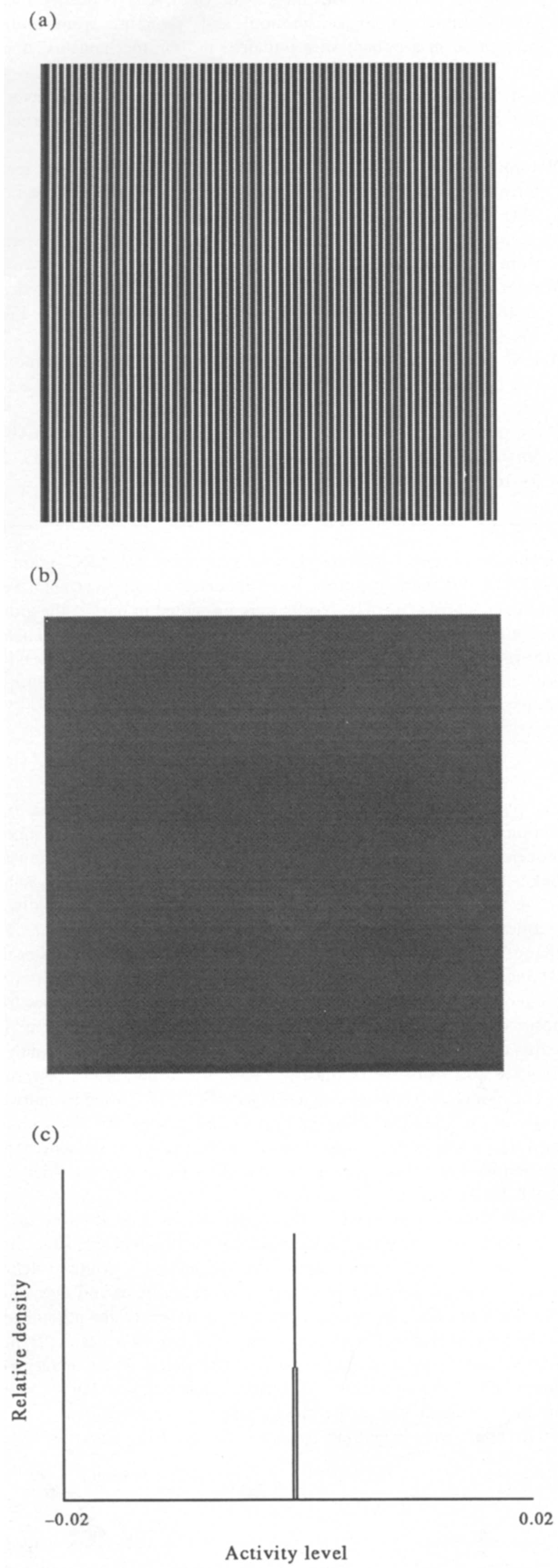

FIGURE 10. Full-field sine wave stimulus and the results of processing it with the first-three stages of the motion model described in the Appendix. (a) Depiction of the first-order stimulus. (b) The activity map resulting from the processing. (c) Histogram of the activity map. There is minimal variation in response level, indicating the lack of a response to this stimulus.

second-order stimuli, having matched thresholds indicates that the first-order and second-order stimuli are driving the system with equal strength.

While it may be argued that a weaker signal can result in the same global-motion threshold (since the strength of both the signal and noise dots would be equally affected) a number of additional results from the present study support our interpretation.* These additional findings are that our first-order dots had the same masking effect as our second-order dots on second-order global-motion extraction. In Experiment 2, adding an additional 50 first-order noise dots had exactly the same impact as adding an additional 50 second-order dots (see Fig. 2, conditions 50S/50F and 100S, respectively). Also, the first-order opposing-vector signal had the same effect on second-order global-motion extraction as would be expected for a second-order opposing-vector signal—namely one-for-one cancellation (see Introduction to Experiment 3). If there was a single global-motion system that was more sensitive to the first-order dots than to the second-order dots, then in both conditions in which the observer had to extract second-order motion in the presence of first-order dots, performance should have been impaired to a greater extent than for the conditions in which the first-order dots were replaced by an equal number of second-order dots. That this was not the case indicates that if there was a single global-motion system, the first- and second-order dots drove it with equal strength, and, of course, the finding that the addition of second-order dots did not impair first-order global-motion extraction counters the possibility of a single global-motion system.

Conclusions

The results of the present study indicate that there exist two systems for the extraction of global-motion signals. One is sensitive only to first-order stimuli while the other is sensitive to both first- and second-order stimuli. Based on the arguments presented above, we propose that the observed sensitivity of the "second-order" system to the first-order stimuli is due to the second-order local-motion detectors being sensitive to the first-order stimuli used in the present study. That is we argue that the first- and second-order motion pathways remain separate up to and including the level in the motion system at which global-motion signals are extracted.

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*This suggestion implies that the signal to noise ratio required in the global motion task should be independent of contrast. As noted in Experiment 1 we have conducted studies investigating the relationship between threshold and contrast for both first- and second-order motion and found that the signal to noise ratio at threshold is dependent on dot contrast up to a saturation level (Edwards & Badcock, 1995).

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APPENDIX

The purpose of this modelling was to demonstrate that the first-order stimuli used in the present study would drive the second-order motion models of the type proposed by Wilson *et al.* (1992) and Zhou and Baker (1993). The model used was a modified version of the Wilson *et al.* filter. The main modification consisted of using halfwave rectification instead of fullwave following the initial filtering stage. This change was made since we have presented evidence which indicates that (at least for global-motion extraction) fullwave rectification does not occur. This evidence consisted of showing that a dot which goes from positive to negative polarity does not drive the motion system (Edwards & Badcock, 1994b). For the stimuli used in the present analysis, fullwave and halfwave rectification gives the same pattern of results.

The model used consisted of a first gabor filter, followed by halfwave rectification, and then refiltering by a second gabor filter. The gaussian used in the second filter was at twice the frequency of the gaussian in the first filter and the sinewave was at half the frequency and orientated at 90° to the one used in the first.

Four stimuli were used: a first-order dot; a second-order dot; a uniform contrast-defined background; and a full-field sinewave. Both the first- and second-order dots were located on a contrast-defined second-order background and the luminance contrasts and sizes of the two dot types and the background were matched to the stimuli used in the present study. The stimuli were generated on a 128×128 pixel matrix. The diameter of the dots was set to 5 pixels. These images were then doubled in size so that the overall image size was 256×256 and the basic element size in the images was a 2×2 pixel array.

The filters were generated by using the following equation:

$$w(x,y) = \exp\left[\frac{(x^2+y^2)}{(2\sigma^2)^2}\right]\cos\left(2\pi\frac{(x\cos\theta)+(y\sin\theta)}{p}+\phi\right)$$

where: w = weighting profile, this function is commonly called a 2-dimensional gabor; x and y = pixel location (values could range between -128 and 128); σ = standard deviation of the gaussian (in pixels); θ = orientation of the sinewave; ϕ = phase angle of the sinewave; p = pixels per cycles of the sinewave.

For the first gabor, these values were set to: $\sigma = 1$; $\theta = 0°$; $\phi = 90°$; $P = 4$.

For the second gabor, they were: $\sigma = 2$; $\theta = 90°$; $\phi = 90°$; $P = 8$.